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Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna

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Summary

1. Large mammalian herbivores are well recognized to play important roles in regulating woody cover and biomass in savannas, but the extent to which browsing ungulates are capable of regulating woody populations in the absence of other disturbances such as fire is unclear. Moreover, the degree to which browser effects on savannas operate through effects on woody plant recruitment vs. mortality has rarely been examined.

2. We conducted a 10-year, replicated herbivore exclusion experiment in a semi-arid savanna in East Africa (mean annual rainfall = 514 mm), where fires have been actively suppressed for decades. Browsers dramatically influenced recruitment, growth and mortality of all size classes of woody vegetation. A decade of herbivore exclusion resulted in a sevenfold increase in recruitment, a 2.5-fold decrease in mortality and a threefold increase in woody biomass inside exclosures, while biomass outside exclosures remained relatively unchanged.

3. At the plant community level, extensive browsing of seedlings by small-bodied ungulates suppressed woody recruitment in this semi-arid system, generating a 'browsing trap' comparable to the 'fire trap' reported for mesic systems. Browsing by large- and medium-bodied ungulates reduced both growth and survival of individuals in larger size classes.

4. At the plant species level, browser impacts were variable. Although browsers negatively influenced recruitment of all species, they had little to no impact on the mortality of some dominant species, resulting in a long-term, browser-driven shift in woody species composition that was largely mediated via their differential effects on plant mortality rates rather than recruitment.

5. *Synthesis*. Our results demonstrate unequivocally that, even in the absence of fire, native browsing ungulates can exert dramatic 'top-down' controls in semi-arid savannas, influencing all aspects of woody plant demography. Besides suppressing woody plant recruitment, browsers can also have substantial cumulative long-term impacts on growth and mortality rates of woody plants, including adults, which can differ between species in ways that fundamentally alter the structure and function of woody vegetation. In semi-arid rangelands, intact communities of native browsing ungulates thus provide a critical ecosystem service by regulating woody cover, and their removal (or extinction) from these systems can lead to rapid woody encroachment.

Key-words: Africa, browsing, dik-dik, elephant, mortality, plant–herbivore interactions, recruitment, shrub encroachment, top-down control

Introduction

Woody vegetation cover and biomass display marked spatial and temporal variation in savanna ecosystems at both local and regional scales (Scholes & Archer 1997; House *et al.* 2003; Sankaran *et al.* 2005). How such variability arises from the direct and interactive effects of climate, edaphic factors, herbivory and fire is still not well understood (Scholes & Archer 1997; Higgins, Bond & Trollope 2000; Sankaran, Ratnam & Hanan 2004; Bond 2008; Holdo, Holt & Fryxell 2009). It is clear that water availability plays a critical role in regulating tree cover and biomass in African savannas, effectively providing a climatic limit to the tree biomass that can be supported at any given site (Bond, Midgley & Woodward 2003; Sankaran *et al.* 2005; Kraaij & Ward 2006; Sankaran, Ratnam & Hanan 2008). However, 'top-down' forces such as herbivory and fire have also been shown to exert significant effects on tree cover and biomass, profoundly altering the structure and composition of many African landscapes (Bond, Midgley & Woodward 2003; Guldemond & van Aarde 2008; Levick & Rogers 2008; Gordijn, Rice & Ward 2012). A

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mechanistic understanding of how fire and herbivory act to control woody vegetation demography and structure is thus central to our understanding of savanna ecology and the management of savanna ecosystems (Holdo, Holt & Fryxell 2009; Gordijn, Rice & Ward 2012).

Herbivory and fire, by reducing survival of seedlings and saplings, impose 'demographic bottlenecks' to tree establishment and prevent savannas from attaining the maximum potential woody cover that would otherwise be possible for a given amount of rainfall (Frost & Robertson 1987; Scholes & Archer 1997; Higgins, Bond & Trollope 2000; Sankaran, Ratnam & Hanan 2004; Sankaran *et al.* 2005). Fires often limit tree cover and biomass by preventing seedling recruitment and sapling maturation to adults, rather than by directly killing adult trees (Hoffmann 1999; Higgins, Bond & Trollope 2000). Although frequent fires can reduce adult tree growth rates (Murphy, Russell-Smith & Prior 2010), they are often assumed to have minimal impacts on the mortality of trees taller than the zone of influence of grass fires (Higgins, Bond & Trollope 2000; Staver *et al.* 2009; but see Williams *et al.* 1999).

Mammalian herbivory and fire are analogous to some degree in their effects on vegetation in that both consume biomass and exert top-down controls on savanna structure (Bond 2005, 2008). However, in contrast to fires, herbivore effects on tree demography have proven harder to generalize across ecosystems (Augustine & McNaughton 1998; Staver *et al.* 2009), and in Africa such effects have rarely been studied in an experimental context. Mammalian browsers have the potential to influence growth and mortality of trees across a range of size classes and life-history stages. Megaherbivores (>1000 kg), including elephants *Loxodonta africana* and giraffe *Giraffa camelopardalis,* can rapidly reduce tree cover by killing mature trees (Dublin, Sinclair & McGlade 1990; Bond & Loffell 2001), while small- and medium-sized browsers can limit adult tree cover by suppressing seedling recruitment and sapling growth (Belsky 1984; Prins & van der Jeugd 1993; Augustine & McNaughton 2004; Moe *et al.* 2009). In Africa, particular emphasis has been given to the role of elephants in regulating tree cover and biomass, but much of this work has relied on observational data (Ben-Shahar 1996; Mapaure & Moe 2009) or been based on modelling analysis (Baxter & Getz 2005; Holdo, Holt & Fryxell 2009). In addition, studies of elephant effects on vegetation often focus on the largest size classes of trees and shrubs, and do not address the potentially important role of smaller, coexisting browsers. In a recent meta-analysis of elephant impacts on savanna vegetation, Guldemond & van Aarde (2008) concluded that elephant impacts on vegetation can range from positive to negative across sites, but these are contingent on rainfall, local environmental conditions and management regimes. For example, elephants had relatively small effects on long-term changes in tree abundance in systems where the dominant acacia species is defended by ant mutualists (Goheen & Palmer 2010). Observational studies have had limited success in separating elephant impacts from the confounding effects of other uncontrolled variables, particularly, fire (Guldemond & van Aarde 2008). Thus, while the potential for browsers to limit tree populations is well recognized, the extent to which browsing mammals are capable of regulating tree populations in the absence of other disturbances such as fire remains less clear.

Several previous studies have concluded that fire and browsing need to act synergistically in order to prevent increases in tree cover. Dublin, Sinclair & McGlade (1990), studying long-term woodland dynamics, concluded that although fires in the Serengeti National Park, Tanzania, were capable of causing shifts from woodland to grassland, elephants by themselves were unable to cause such shifts. However, once an external perturbation such as fire reduced tree densities, elephants were then capable of maintaining the system in that state. Simulation models of vegetation dynamics in the Kalahari woodlands of western Zimbabwe suggest that elephants are the primary drivers of woodland change in this system, capable of driving the vegetation from woodland to a scrubland phase, but not to grassland (Holdo 2007). Fires, although incapable of independently suppressing woodland regeneration, nevertheless appear to play important roles in maintaining the system in an open state (Holdo 2007). Similarly, models of tree population dynamics in the Hluhluwe iMfolozi Park in South Africa suggest that fire alone is insufficient to suppress tree cover and that a combination of fire and browsing is required to prevent the emergence of dense thickets in this system (Staver *et al.* 2009). Thus, while it is clear that browsing can interact with other disturbances such as fire to regulate vegetation dynamics, the extent to which browsers are capable of limiting savanna tree cover in the absence of other disturbances remains unknown. Isolating the effects of browsing on savanna tree dynamics requires long-term, controlled herbivore exclusion experiments, which are rare in Africa (Bond 2008).

Here, we report results from a decade-long, replicated herbivore exclusion experiment in a semi-arid savanna in East Africa where fires have been actively suppressed for decades. A primary objective was to understand the role of native ungulates in regulating woody plant dynamics in savannas where the native fauna have been allowed to coexist with cattle. Previous short-term research at this site found that levels of defoliation are greatest for saplings <0.5 m tall due to intensive, year-round browsing by small ungulates, particularly dik-dik (*Madoqua* sp.; Augustine & McNaughton 2004). Shrubs that escaped above the foraging height of dik-dik experience low browsing intensity until reaching larger height classes (>2.5 m), and then begin to experience high levels of defoliation and stem damage by elephants. These patterns, combined with results from short-term exclosure measurements (Augustine & McNaughton 2004), indicate that the combined effects of small and large browsers could regulate shrub dynamics in a similar manner to the interactive effects of fire and large browsers, with small browsers replacing fire as the critical bottleneck suppressing woody seedling and sapling establishment. Our specific objectives were to (i) quantify the long-term effects of browsers on shrub dynamics in the absence of external perturbations such as fire, (ii) evaluate the extent to which browsers of different body sizes imposed 'bottlenecks' on different size classes of shrubs and (iii) determine whether browsers differentially affect the recruitment, growth and mortality of shrub species that vary in the type and level of mechanical defence against herbivores.

STUDY AREA

The study was conducted at the Mpala Research Centre and associated Mpala Ranch (MRC) in north-central Laikipia, Kenya (37°53 E′, 0°17 N′). Study sites were underlain by well-drained, moderate to very deep, friable sandy loams developed from metamorphic basement rocks (Ahn & Geiger 1987) and occurred at elevations of *c.* 1700 m. Long-term mean annual rainfall (1972–2009) for a gauge located near the centre of our study area was 514 mm, and for the period 1999–2009 averaged 493 mm. However, our study sites are distributed along a precipitation gradient (Augustine 2003), with a gauge located near the most mesic study site recording an average of 593 mm annually during 1999–2009. Rainfall in the area typically occurs in a trimodal fashion with a consistent dry season between January–March, and wet seasons during April–May, August and October. Vegetation in the area is characterized by an *Acacia*-dominated bushland community and a discontinuous layer of perennial grasses (Augustine 2003). The shrub layer is dominated by *Acacia mellifera*, *Acacia etbaica*, *Acacia brevispica* and *Grewia tenax* (Augustine & McNaughton 2004). Analyses of aerial photos from 1961 and 1969 (D. J. Augustine, pers. obs.) combined with reports from long-term residents of the district indicate shrub cover has increased over the past half century, reaching an average cover of 28% in north-central Laikipia in 1998 (Augustine 2003).

The most common native browsers and mixed feeders are impala *Aepyceros melampus* (*c.* 20 km^{-2}), dik-dik (*c.* 140 km^{-2}) and elephant (*c.* 1.7 km^{-2}; Augustine 2010). Impala and dik-dik are year-round residents, while elephant migrate into the area during wet seasons and are largely absent during dry seasons (Thouless 1995; Augustine 2010). Eland *Taurotragus oryx*, giraffe *Giraffa camelopardalis* and greater kudu *Tragelaphus strepsiceros* are also present at low densities. Analyses of ^{13}C in dung samples in the study area have shown that elephant, eland and dik-dik are nearly pure browsers in both wet and dry seasons; impala are browsers in the dry season but significantly increase grass consumption in the wet season (Augustine 2010). Predators occurring in the area during the study include spotted hyaena (*Crocuta crocuta*), lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*) and striped hyaena (*Hyaena hyaena*). Wild dogs (*Lycaon pictus*) were extirpated from the area in the 1980s and were not present during 1999–2001; they recolonized the study area in 2002 and have been increasing in abundance since then (Woodroffe *et al.* 2007; Woodroffe 2011).

Materials and methods

Herbivore exclosures (70 × 70 m) and adjacent paired control plots were established in *Acacia*-dominated bushland areas at each of three study sites at MRC in 1999. Exclosures were protected with a 11-strand, 3-m tall electrified fence following the design of Young *et al.* (1998) with additional mesh and electrified wires from 0 to 0.5 m height (Augustine & McNaughton 2004). Fences were effective in excluding all large herbivores ranging in size from dik-diks to elephants, but some incursions by dik-dik did occur during 2007–2008 due to reduced frequency of fence checks during this time period. At the time of fence establishment in 1999, we mapped all individual trees and shrubs >0.5 m tall within a 50 × 50 m area in each exclosure and paired control sites and measured their basal area (at 15 cm above-ground level, including all stems on multistemmed individuals), canopy dimensions (maximum length and width in the cardinal directions) and height. In addition, soil properties and herbaceous species composition and diversity were characterized at all sites. Further details of the experimental design can be found in Augustine & McNaughton (2004). Plots were censused again in 2002 and 2009, with all shrubs and trees >0.5 m mapped and remeasured in terms of basal area, canopy dimensions and height. Above-ground woody biomass in plots was estimated based on the relationship derived by Epp, Herlocker & Peden (1982) where mass in kg = [(7.49 × crown diameter in m) − 7.76] (Epp, Herlocker & Peden 1982; Augustine & McNaughton 2004); this equation provides biomass estimates that are intermediate compared with other reported regression equations for Kenyan shrublands (Deshmukh 1992; Augustine & McNaughton 2004).

We used paired *t*-tests to evaluate effects of browser exclusion on woody basal area, above-ground live biomass, recruitment and mortality at the whole-plot level over the 10-year-treatment period. Recruitment here refers to all new individuals >0.5 m tall recorded in the 2009 census but not the 1999 census. It is thus an integrated measure of effective recruitment over 10 years and does not include data on individuals that recruited and died between the census dates. Mortality similarly refers to the fraction of all individuals present in the 1999 census that had died by the 2009 census.

To better understand browser effects on shrub population dynamics in this system, changes in biomass, basal area, recruitment and mortality were analysed separately for the dominant species in our study sites: *Acacia mellifera*, *A. etbaica* and *Grewia tenax*. Effects of browser exclusion on changes in woody basal area, biomass, recruitment and mortality were analysed using a split-plot ANOVA with browsing as the whole-plot factor and species identity as the subplot factor. When interactions were significant, planned contrasts using standard errors and degrees of freedom calculated for split-plot designs (Keuhl 2000) were used to compare responses of individual species within and across browsing treatments. Data on recruitment and mortality were transformed to meet the assumptions of normality. We also evaluated mortality as a function of initial tree size for all species combined and for *A. mellifera* and *A. etbaica* separately, using a split-plot ANOVA with browsing as the whole-plot factor and size class as the subplot factor. Individuals were grouped into three classes for the analysis based on their initial heights in 1999: small (>0.5 m and <1.5 m), medium (≥1.5 m and <2.5 m) and large (≥2.5 m). We did not include data for *G. tenax* for the latter analysis as individuals of the larger size classes (>1.5 m) were absent at one of our sites resulting in an unbalanced design.

We also evaluated the effects of browsing treatments on the growth patterns of individual shrubs and trees. The analysis was restricted to individuals that were present at both the 1999 and 2009 census. Effects of browser exclusion on change in height and basal area of trees from 1999 to 2009 were evaluated as a function of initial size class (see above) using a split-plot ANOVA with browsing as the whole-plot factor and size class as the subplot factor. Finally, we also used data from our control plots to determine if damage, as indexed by the proportion of individuals showing signs of browsing, varied by species and by size class. We also calculated a preference or selection ratio d_i/n_i for the dominant species within plots, and at the landscape scale by pooling data across all plots, where d_i represents the proportion of damaged plants represented by species *i*, and n_i the proportion of species *i* in the plot (Crawley 1983; Holdo 2003) to determine if damage on different species was higher, lower or in proportion to their availability in the landscape.

Results

PLOT LEVEL RESPONSES

The decade-long exclusion of native browsing ungulates dramatically influenced woody vegetation attributes in plots (Fig. 1). Over the 10-year period, basal area and woody biomass increased by nearly two and threefold, respectively, in plots where browsers were excluded (basal area: $t = -6.93$, $P = 0.02$; biomass: $t = -5.89$, $P = 0.028$), but remained unchanged in plots exposed to browsing ($P > 0.05$ for both basal area and biomass; Fig. 1). Browser exclusion resulted in nearly a sevenfold increase in shrub sapling recruitment rates into the >0.5 m height category ($t = 5.42$, $P = 0.016$; Table 1) and a 2.5-fold decrease in overall mortality rates of shrubs >0.5 m tall ($t = 3.77$, $P = 0.032$, Table 1). Shrub recruitment into the >0.5-m-height class in the presence of browsers, as measured over the first 3 years of the experiment (1999–2002: 27.6 ± 8.1 individuals ha^{-1} year^{-1}) was similar to the rate measured in the last 7 years of the experiment (2002–2009: 29.7 ± 24.0 individuals ha^{-1} year^{-1}, $t = -0.09$, $P = 0.47$). However, in the unbrowsed treatment, the recruitment rate in the last 7 years (2002–2009: 202.1 ± 11.7 shrubs ha^{-1} year^{-1}) was higher compared with the first 3 years (146.7 ± 11.5 shrubs ha^{-1} year^{-1}, $t = -7.12$, $P = 0.009$).

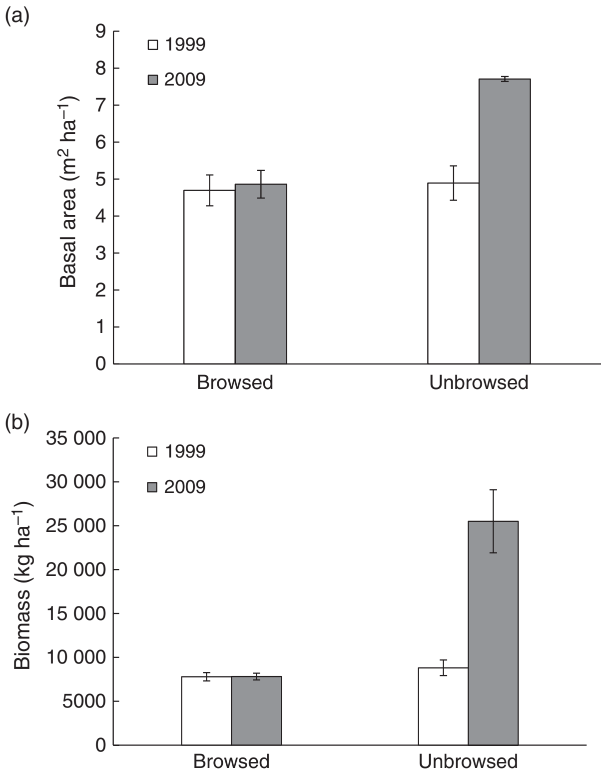

Fig. 1. Decadal changes in (a) total basal area (m^2 ha^{-1}) and b) biomass (kg ha^{-1}) of browsed and unbrowsed plots. Basal area and biomass values have been scaled up from the plot level (70 × 70 m) and are reported on a per hectare basis. Error bars represent ± 1 SE.

Table 1. Effects of browsers on woody plant recruitment and mortality at the whole-plot level (means with 1 SE in parentheses) at Mpala Research Centre based on 10 years of herbivore exclusion

	Treatment	
Response variable	Browsed	Fenced
Shrub recruitment into the >0.5-m height class (number ha^{-1} 10 year^{-1})		
All species combined	278.6 (181.9)	1832 (111.3)
Acacia mellifera	21.3 (1.3)	613.3 (63.3)
Acacia etbaica	29.3 (23.6)	548.0 (293.1)
Grewia tenax	30.7 (20.7)	302.7 (124.8)
Other species	197.3 (173.4)	368.0 (96.9)
Mortality rates (% 10 year^{-1}) of shrubs >0.5 m tall (all size classes combined)		
All species combined	20.8 (3.6)	7.9 (2.3)
A. mellifera	20.6 (5.3)	6.1 (1.3)
A. etbaica	11.9 (0.2)	10.0 (6.4)
G. tenax	38.3 (11.6)	7.7 (1.3)
Other species	27.7 (8.6)	8.6 (1.5)

SPECIES LEVEL RESPONSES

In the absence of browsers, all dominant species showed substantial increases in basal area over the 10-year period (Fig. 2a). We found no net change in the basal area of most species in browsed plots over the 10-year period, with the exception of *A. etbaica* whose basal area increased even in the presence of browsers (Fig. 2a). The three dominant species (*A. mellifera*, *A. etbaica* and *G. tenax*) differed in the magnitude of their basal area responses to browser exclusion (Fig. 2a; Browsing × Species interaction: $F_{2,8} = 5.77$, $P = 0.028$), with significant differences between browsed and unbrowsed plots detected only for *A. mellifera* (planned contrasts; $P < 0.05$). Unlike the patterns observed for basal area, biomass of all species increased significantly following browser exclusion (browsing: $F_{1,2} = 87.89$, $P = 0.011$; Browsing × Species interaction: NS). As with basal area, there were no detectable changes in biomass of species in browsed plots over the 10-year period, with the exception of *A. etbaica* whose biomass increased in browsed plots (Fig. 2b).

Effects of browsing on recruitment into the >0.5 m height class were similar across species; all dominant species showed significantly higher recruitment following browser exclusion (Fig. 3a; browsing: $F_{1,2} = 231.28$, $P = 0004$; Species and Browsing × Species: NS). Browser effects on tree mortality

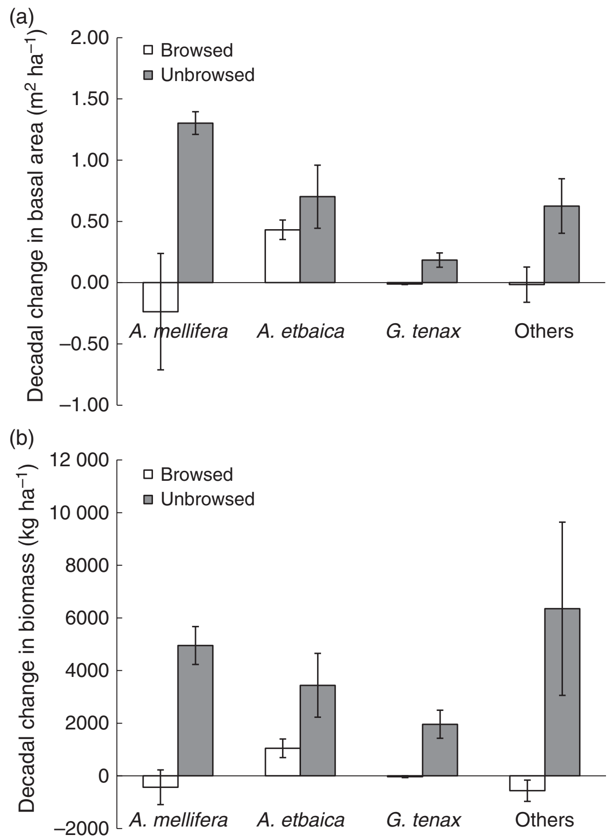

Fig. 2. Decadal change in (a) basal area (m^2 ha^{-1}) and (b) biomass (kg ha^{-1}) of dominant species in browsed and unbrowsed plots. Basal area and biomass values have been scaled up from the plot level (70 × 70 m) and are reported on a per hectare basis. Error bars represent ± 1 SE.

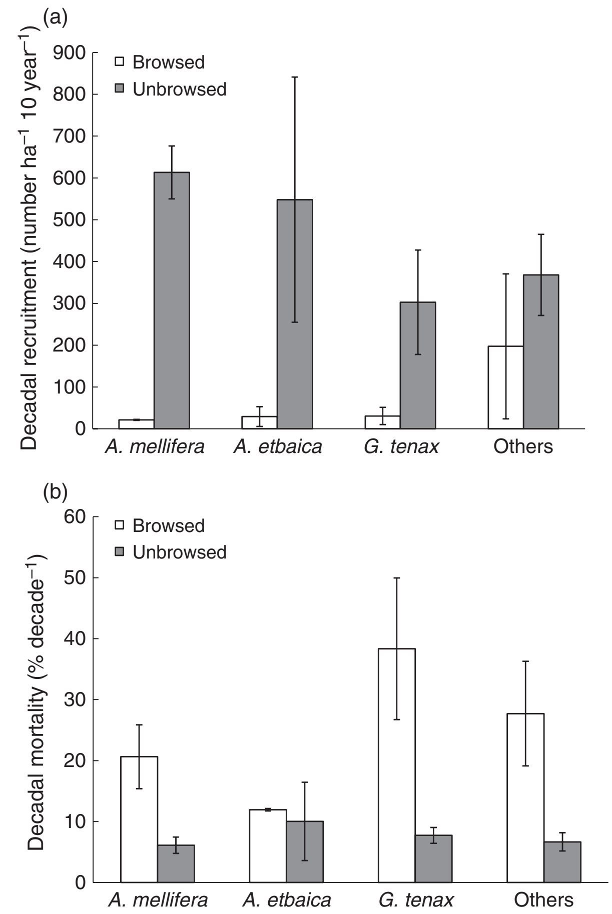

Fig. 3. (a) Decadal recruitment (number ha^{-1}) and (b) decadal mortality (% $decade^{-1}$) of the dominant species in browsed and unbrowsed plots. Estimates of recruitment have been scaled up from the plot level (70 × 70 m) and are reported on a per hectare basis. Bars represent ± 1 SE. For comparison, we also present data for all other species combined.

patterns differed among species (Fig. 3b; Species × Browsing: $F_{2,8}$ = 3.13, P = 0.09; browsing: $F_{1,2}$ = 18.18, P = 0.0501; species $F_{2,8}$ = 4.72, P = 0.04). Overall, mortality rates under browsing were highest for *G. tenax* (Fig. 3b); significantly higher than *A. etbaica* (planned contrasts; $P < 0.05$) and marginally higher than *A. mellifera* ($P < 0.10$). In the absence of browsing, mortality rates did not differ between the dominant species, averaging about 7.9% per decade (Fig. 3b, Table 1). Protection from browsing significantly reduced mortality rates for both *A. mellifera* and *G. tenax*, but not for *A. etbaica* (Fig. 3b).

MORTALITY BY SIZE CLASS

In general, mortality decreased as a function of tree size in both browsed and unbrowsed treatments (Fig. 4a), with the smallest size classes (0.5–1.5 m) showing significantly higher mortality rates than the largest size class (>2.5 m) within each browsing treatment (planned contrasts, $P < 0.05$). At the whole-plot level, browsers had differential impacts on the mortality of different size classes of shrubs (Fig. 4a; Browsing × Size interaction: $F_{2,8}$ = 4.38; P = 0.051). Protection from browsing significantly reduced mortality rates for small- (0.5–1.5 m) and intermediate-sized individuals (1.5–2.5 m; planned contrasts, $P < 0.05$), but did not influence mortality of larger trees (>2.5 m; planned contrasts: NS).

Mortality of the dominant species varied as a function of size (Fig. 4b–d). In the presence of browsers, *A. mellifera* had consistently high mortality rates across all size classes, averaging *c.* 20% per decade (Fig. 4b). Mortality of *A. mellifera* was lower for all size classes in the absence of browsing, particularly for the intermediate-sized individuals (Fig. 4b; Browsing $F_{1,2}$ = 15.76; P = 0.057; Size and Browsing × Size: NS). In contrast, browsing had no effect on mortality rates of *A. etbaica* for any size class (Fig. 4c; Browsing and Browsing × size: NS), although mortality decreased as size increased (Fig. 4c; Size $F_{2,8}$ = 4.667; P = 0.04). Like *A. mellifera*, *G. tenax* had consistently high mortality rates, averaging around 40% per decade for all size classes when browsed. Removal of browsing reduced mortality rates substantially, to 10%. *G. tenax* mortality did not vary by size class.

BROWSER EFFECTS ON GROWTH AND DEMOGRAPHY

Browsing had a significant impact on both height and basal area increment of trees over the 10-year period (Fig. 5a,b).

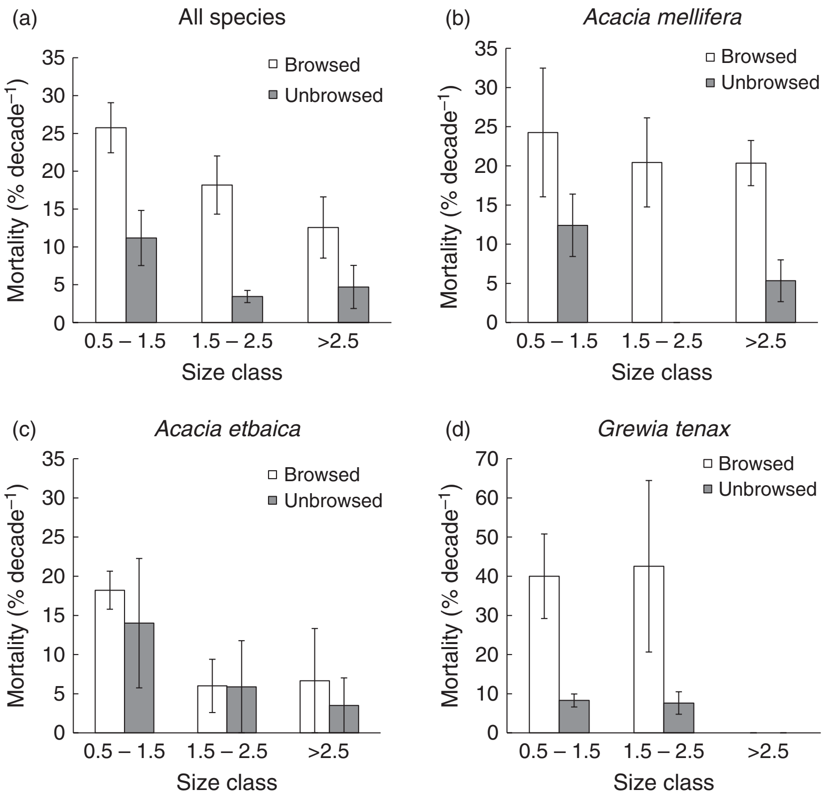

Fig. 4. Browser effects on decadal mortality (% decade^{-1}) for different shrub size classes for (a) all species combined, (b) *Acacia mellifera*, (c) *Acacia etbaica*, and (d) *Grewia tenax*. Bars represent ± 1 SE.

Across all size classes, height increments of trees were significantly greater in unbrowsed plots compared with browsed plots (Browsing: $F_{1,2}$ = 141.2, P = 0.007; Browsing × Size: $F_{2,8}$ = 2.36, NS; Fig. 5a). In contrast to the unbrowsed condition (where height increments were positive), tree heights of small- and medium-sized trees (<2.5 m tall) in browsed plots remained largely unchanged over the 10-year study period (Fig. 5a). In contrast, individuals of the tallest size classes (>2.5 m) showed a net decrease in height from 1999 to 2009, largely as a result of elephant damage (Fig. 5a).

We also assessed whether growth rates of the smallest shrub height class (0.5–1.5 m) changed when viewed over the first 3 years of the experiment (1999–2002; no wild dogs) vs. the last 7 years of the experiment (2002–2009, wild dogs present). In browsed plots, net height growth of *A. mellifera* in this height class was 0.019 + 0.018 m year^{-1} (mean + 1 SE) for the first 3 years, as compared to 0.001 + 0.007 m year^{-1} for the last 7 years (2002–2009: test for difference in growth rate between time periods: t = 1.36, P = 0.31). For *A. etbaica*, net height growth in browsed plots was 0.0 + 0.066 m year^{-1} in the first 3 years, as compared to 0.02 + 0.009 m year^{-1} over the last 7 years (t = 1.04, P = 0.41). Thus, there was no evidence that net height growth increased for either shrub species in the presence of browsers during the latter 7 years of the experiment. In contrast to the browsed treatment, net height growth rate of unbrowsed *A. mellifera* doubled from 0.076 + 0.014 m year^{-1} in the first 3 years to 0.17 + 0.03 m year^{-1} in the last 7 years (t = 3.56, P = 0.070), and net height growth rate of unbrowsed *A. etbaica* nearly tripled from 0.066 + 0.02 m year^{-1} during the first 3 years to 0.22 + 0.02 m year^{-1} in the last 7 years (t = 8.02, P = 0.015).

Browsers also influenced basal area increments of trees, but only for the largest size classes (Browsing × Size: $F_{2,8}$ = 8.97; P = 0.009; Fig. 5b). Over the 10-year period, basal area of small- and medium-sized trees increased to the same extent in both browsed and unbrowsed plots (Fig. 5b, planned contrasts P > 0.05). The basal of large trees (>2.5 m) increased dramatically when browsers were excluded, but remained unchanged in the presence of browsing (Fig. 5b).

When viewed in terms of the overall woody plant community, our results show that browsers dramatically reduced the probability that a shrub will remain in the largest size class (>2.5 m) and increased the probability that shrubs will remain in the smaller size classes (0.5–1.5 m and 1.5–2.5 m; Fig. 6a, b). This shift occurred due to browser effects on nearly all transition probabilities, including increased mortality rates in all size classes, reduced transition rates to larger size classes and increased probability that shrubs will revert to smaller size classes (Fig. 6a,b). These findings reveal a strong browser-induced shift in the size-class distribution of the woody plant community occurring along with the overall reduction in woody biomass and basal area. Transition probabilities for *A. mellifera* were qualitatively similar to that observed for all species combined (data not shown). However, transition probabilities for *A. etbaica* in browsed plots differed from the overall plant community when browsed and were similar to probabilities documented for the overall plant community in unbrowsed plots (Fig. 6c).

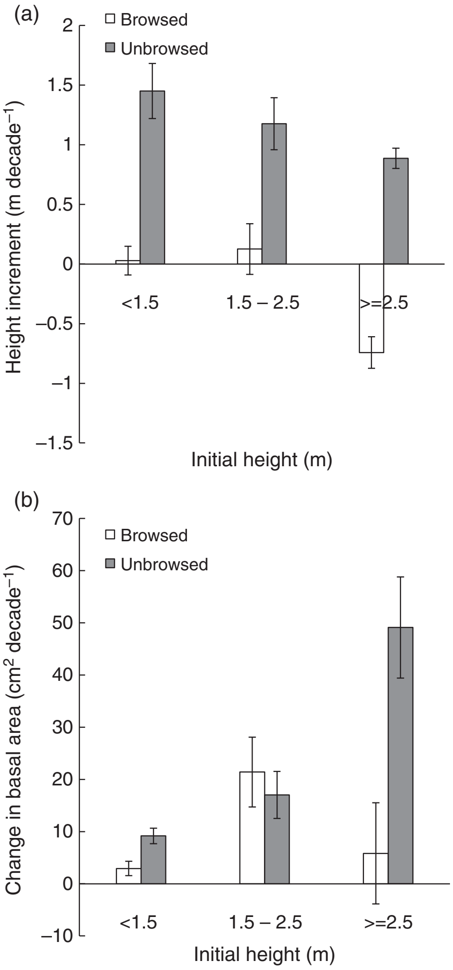

Fig. 5. a) Height and b) basal area increment of trees from 1999 to 2009 as a function of initial size in the presence and absence of browsing. Data are for all species combined. Bars represent ± 1 SE.

HERBIVORE DAMAGE BY SPECIES IN CONTROL PLOTS

Across all species and size classes, damage – as indexed by the proportion of individuals in plots showing signs of browsing – ranged from 23% to 40% across sites. Damage was consistently high across plots for *A. mellifera* (proportion damaged ranged from 41% to 43%), but much more variable for *A. etbaica* (range: 7–49%) and *G. tenax* (range: 0–42%), resulting in a lack of consistent differences between species in damage sustained ($F_{2,4} = 1.149$, $P = 0.40$). Across all species, damage was marginally lower in the smallest size class (0.5–1.5 m) when compared with the larger size classes (size: $F_{2,14} = 3.26$, $P = 0.069$; Species and Species × Size: NS). At the plot level, preference or selection ratios for the different species mirrored those observed for damage and were consistently high for *A. mellifera* (range: 1.01–1.8) and much more variable for *A. etbaica* (range: 0.3–1.2) and *G. tenax* (0–1.74). At the landscape scale, when data were pooled across plots, *A. mellifera* showed disproportionately high levels of damage (preference ratio = 1.25), while *A. etbaica* tended to be avoided by herbivores (Selection ratio = 0.63), and *G. tenax* was damaged in proportion to its availability (Selection ratio = 0.99).

Discussion

Results from our decade-long herbivore exclusion experiment indicate that large mammalian herbivores can exert substantial 'top-down' controls in savannas, influencing all demographic stages of woody vegetation and dramatically altering the structure and function of savanna vegetation (Fig. 6). Recruitment of woody vegetation into the smallest size class and growth transitions to larger size classes were lower, and mortality and reversion to smaller size classes higher, in browsed compared to unbrowsed sites. Overall, exclusion of large herbivores resulted in a nearly sevenfold increase in shrub and tree recruitment into the >0.5 m height category, a 2.5-fold decrease in mortality across all size classes and a threefold increase in woody biomass within a decade in this semi-arid savanna system.

Several factors collectively contribute to the strong browser-mediated suppression of woody biomass at our study site. First, the site supports an abundant and diverse assemblage of browsing and mixed feeding ungulates (Augustine 2010). Total herbivore biomass densities, both native and domestic, exceeded 7500 kg m^{-2} and were comparable to, if not higher than, other similar habitats in protected areas and game reserves (Augustine 2010), ensuring high levels of chronic, year-round browsing on vegetation. A diverse community of native carnivores including lions, spotted hyaena, leopard, cheetah and striped hyaena occurs in the study area (Frank, Woodroffe & Ogada 2005), suggesting the lack of a cascading predator effect on shrub–browser interactions. However, African wild dogs were extirpated from our study area in the 1980's and absent at the start of our experiment during 1999–2001 (Woodroffe 2011). Wild dogs recolonized the study area in 2002 and their density increased steadily during 2002–2009. Wild dog diets at our study site consisted largely of dik-dik and impala (Woodroffe *et al.* 2007; Woodroffe 2011). We found that browser effects on the recruitment of shrubs into the 0.5–1.5 m height class were similar during the first 3 years of the experiment 1999–2002 (27.6 ± 8.1 individual ha^{-1} year^{-1}; Augustine & McNaughton 2004) as for last 7 years (29.7 ± 24.0 individual ha^{-1} year^{-1}) and for the full decade (27.9 ± 18.2 individuals ha^{-1} year^{-1}; Fig. 6). Furthermore, growth rates of both *A. mellifera* and *A. etbaica* shrubs in the 0.5–1.5 m height class were not consistently higher during the latter 7 years when compared with the first 3 years of the experiment. Both results suggest that at least during the period of initial restoration of the wild dog population, browser control of woody plant dynamics continues to be substantial. If wild dogs suppress dik-dik more than impala, another possible explanation for our results may be a compensatory increase in browsing pressure in low height classes by impala in response to reduced dik-dik density.

Intensive, year-round chronic browsing of seedlings <0.5 m tall by small-bodied ungulates, particularly dik-dik, constrains woody biomass by generating a 'browsing trap', which, our results suggest, is similar to a 'fire trap' (Fornara & Du Toit 2008; Staver *et al.* 2009). Although different plant species may differ in their regrowth responses to fire and herbivory in

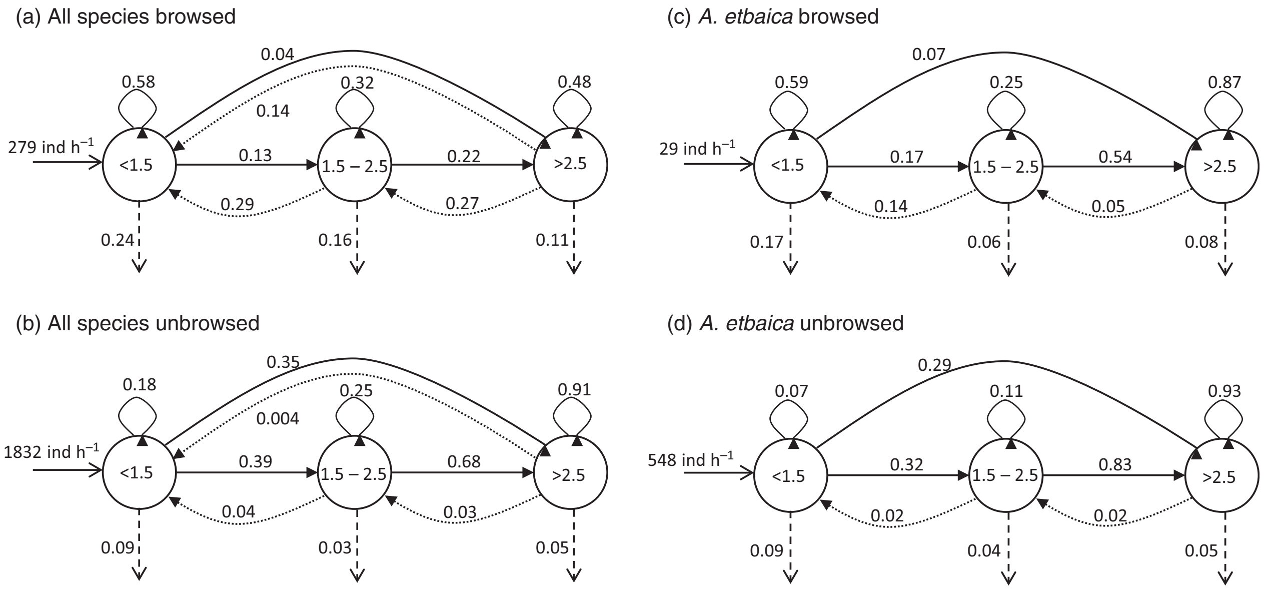

Fig. 6. Woody plant demography in the presence and absence of browsing for all species combined (a, b) and for *Acacia etbaica* (c, d). Circles represent different size classes. Solid lines denote recruitment, survival within a size class and transitions to larger size classes. Reversions to smaller size classes are represented by dotted lines, and mortality using dashed lines. There were no reversions from the largest to the smallest size class for *A. etbaica* in either browsed or unbrowsed plots. Rates of recruitment into the <1.5-m height class are shown as number of individuals per hectare over a decade. All other values represent probabilities estimated by pooling data across all plots for all species combined.

the short-term (Hean & Ward 2012), our results indicate that over the long-term, chronic herbivory can impose severe demographic bottlenecks at the whole plant community level, similar to fires. The sevenfold increase in shrub recruitment into the >0.5 m height category following browser exclusion is testimony to the severity of the demographic bottleneck generated by this 'browsing trap' at our study site, even given the changes in the predator community discussed previously. We also note that unlike large ungulates, dik-dik populations can be surprisingly stable in the face of significant interannual climatic fluctuations including extreme droughts and above-average rainfall years (Augustine 2010), ensuring temporal constancy of this demographic bottleneck on shrub populations. As the wild dog population has continued to increase in this region (Woodroffe 2011), a key question is whether dik-dik populations can eventually be reduced to the point where the shrub recruitment bottleneck is removed.

Individuals that escaped the browsing trap imposed by smaller bodied ungulates and recruited into the >0.5 m height categories nevertheless continued to be impacted by larger bodied herbivores such as impala and elephant. Mortality rates of woody plants in the presence of browsers were consistently higher for all size classes >0.5 m (Fig. 4a), and height increments over the decade were negative (>2.5 m size class) or near zero (0.5–2.5 m size class; Fig. 5a), when browsed. Similar impacts on shrub growth and mortality of medium-sized herbivores such as impala (Belsky 1984; Sharam, Sinclair & Turkington 2006; Moe *et al.* 2009) and elephants (Barnes 2001; Birkett & Stevens-Wood 2005; Mapaure & Moe 2009) have been reported from other systems. Cumulatively, browser effects on recruitment, growth and mortality at our study site reduced the change in net shrub densities to near zero, with the result that woody basal area and biomass at the landscape scale remained unchanged over the decade (Fig. 1). In contrast, woody basal area and biomass increased two and threefold, respectively, inside exclosures (Fig. 1), highlighting the potential for strong herbivore control of woody vegetation in this system even in the absence of other synergistic disturbances such as fire. We suspect that such strong herbivore control of woody biomass in the absence of fire is likely to be a characteristic of arid and semi-arid savannas, rather than mesic savannas. Higher growth rates of woody vegetation, combined with typically lower abundance and biomass of smaller ungulates in more mesic areas (Ritchie & Olff 1999), suggest that shrubs and trees are more likely to escape the browsing trap in the absence of frequent fires, thus limiting the potential for herbivores by themselves to suppress woody biomass.

Although total woody basal area and biomass in browsed sites did not change over the decade (Fig. 1), our results indicate that browser effects varied by species with potential implications for the future species composition of the shrub community. In particular, browsers had weak impacts on the dynamics of *A. etbaica* when compared with the other dominant species in the community (Fig. 6). Browsing on *A. etbaica* was quite variable across sites, and although nearly 50% of *A. etbaica* individuals showed signs of browsing damage at one of our sites, our results indicate that at the landscape scale *A. etbaica* was damaged at lower proportions than its availability (Selection ratio = 0.63). Furthermore, although browsers significantly influenced recruitment of *A. etbaica* individuals into the >0.5 m size class (Fig. 3a), they had virtually no impact on mortality of *A. etbaica* individuals >0.5 m tall (Figs. 3b, 4c and 6) unlike other species.

Consequently, *A. etbaica* was the only dominant species to show a net increase in both basal area and biomass outside exclosures over the decade (Fig. 2), suggesting a long-term browser-induced directional shift in woody species composition towards dominance by *A. etbaica*.

Previous studies that have investigated effects of browsing mammals on woody plant dynamics in African savannas have yielded divergent results, with some studies finding significant effects on components of woody plant communities (Augustine & McNaughton 2004; Goheen *et al.* 2007; Fornara & Du Toit 2008; Moe *et al.* 2009; MacLean *et al.* 2011), others demonstrating negligible or weak effects on savanna structure (Guldemond & van Aarde 2008; Kalwij *et al.* 2010; Scogings *et al.* 2012), and several others concluding that herbivore effects on woody vegetation, particularly in mesic sites, are most pronounced when coupled with other disturbances such as fire (Dublin, Sinclair & McGlade 1990; Barnes 2001; Staver *et al.* 2009; Shannon *et al.* 2011; Vanak *et al.* 2012). However, most previous studies have either tended to be short-term or have focussed on specific life stages or subsets of the plant and herbivore assemblage (but see MacLean *et al.* 2011), and longer-term experimental studies that explicitly evaluate herbivore effects on all aspects of woody plant demography are rare (Midgley, Lawes & Chamaillé-Jammes 2010). Although we did not specifically quantify the effects of herbivory on the early demographic stages of trees including seed output, germination, and the survival and growth of the smallest size classes (<0.5 m) in this study, previous shorter-term work in the same exclosures have shown that browsers are capable of significantly reducing growth rates of twigs <0.5 m (Augustine & McNaughton 2004), but have little to no influence on seed outputs of the dominant acacias *A. mellifera* and *A. etbaica* for up to 5 years following herbivore exclusion (Young & Augustine 2007). We also did not quantify the indirect effects of herbivores on woody dynamics in our study. Indirect effects of herbivores, such as those arising from changes in grass biomass and the strength of tree–grass competition (Riginos & Young 2007; Riginos 2009), as well as the abundance of other cryptic consumers such as rodents, could be important in some systems for early demographic stages of trees such as seed and seedling survival (Goheen *et al.* 2004; MacLean *et al.* 2011). While future studies would benefit from a quantification of both direct and indirect effects on different demographic stages of trees, our results suggest that direct effects of herbivores, particularly on seedling and sapling stages, are nevertheless substantial.

Our results contrast with similar long-term experiments conducted on more nutrient-rich, high-clay (black cotton) soils occurring in the region, which are characterized by near monodominant stands of the myrmecophyte whistling-thorn acacia *A. drepanolobium* (Young *et al.* 1998). In these *A. drepanolobium* stands, woody vegetation responses to herbivore exclusion have been much weaker compared with our study. For example, tree densities in black cotton plots exposed to herbivores were 26% lower on average than those from which wild ungulates had been excluded for >15 years (MacLean *et al.* 2011), compared with 40% at our site after 10 years of herbivore exclusion. Similarly, Goheen & Palmer (2010) reported no change in the cover of *A. drepanolobium* on black cotton soils inside and outside exclosures over a 5-year period, despite increases in elephant densities during this time. Presumably, the high investment by *A. drepanolobium* in both physical (long, straight spines) and associational defences involving their ant mutualists (Goheen *et al.* 2007; Goheen & Palmer 2010) precludes quick release following the removal of herbivory. In addition, the *A. drepanolobium* system supports only a low density of small ungulates, consisting mainly of steenbuck (*Raphicerus campestris*; Young *et al.* 1998). Together, these results suggest that the outcome of herbivore exclusion for woody vegetation dynamics is contingent on characteristics of the ungulate community, and on the antiherbivore strategies employed by the trees themselves. Our results show that in savannas where the dominant shrubs (such as *A. mellifera* and *A. etbaica*) rely on spines as their primary defence mechanism, woody vegetation can be strongly suppressed by the combined effects of small browsers that are nimble enough to remove leaves between spines, and large browsers capable of consuming both leaves and spines. A key unresolved issue is why these species (in this growth environment) do not invest in additional defence mechanisms such as secondary chemicals or ant symbionts. The differential responses to browsing that we documented for the three dominant species sheds some light on this question, as they represent a gradient of investment in herbivore defence: *G. tenax* has no spines, *A. mellifera* has only short, recurved spines, and *A. etbaica* employs a combination of long, straight spines and short, recurved spines. The investment in both types of spines by *A. etbaica* is consistent with an increase in the relative abundance and correspondingly lower herbivore damage, of this species over the decade. Over longer time-scales, a shift towards monodominance of *A. etbaica* (similar to the monodominance of *A. drepanolobium* on black cotton soils) may increase the resilience of the shrub layer to browsing (also see Gordijn, Rice & Ward 2012).

Our results highlight the importance of long-term experimental studies for a detailed understanding of herbivore effects on woody vegetation dynamics and demography (Midgley, Lawes & Chamaillé-Jammes 2010). For example, measurements made 3 years following the start of the experiment revealed a sixfold increase in recruitment into the >0.5 m size class inside exclosures, but few detectable differences in growth increments or mortality rates of individuals >0.5 m tall (Augustine & McNaughton 2004). This is in contrast to results based on a decade of monitoring which indicate a sevenfold increase in recruitment as well as substantial impacts of herbivores on growth and mortality across all size classes. Savanna trees are typically long-lived, and tree dynamics in arid and semi-arid savannas often tend to be 'event-driven', where the timing and magnitude of episodic rainfall events drives plant growth, mortality and other ecosystem processes. Consequently, short-term studies are likely to miss important recruitment or die-back events and thus incorrectly estimate demographic parameters and transitions. Our findings show that browsers maintain the woody layer in a low-density state dominated by individuals in the 0.5–1.5 m and 1.5–2.5 m height classes, while removal of browsers generates a high-density state dominated with a size structure increasingly skewed towards individuals >2.5 m (Fig. 6). These shifts occur not just because browsers reduce rates of plant growth and recruitment, but also because over longer time-scales, browsers significantly increase rates of mortality for the more palatable woody species (Fig. 3). At the same time, mortality of the most defended species, *A. etbaica*, was unaffected by browsers even over a decade, again indicating a long-term shift towards dominance of the species should browsing continue at current levels.

Understanding the contexts under which large mammalian herbivores can regulate plant populations is of significant practical importance, both for the effective management of savannas, and for predicting their responses to altered browsing regimes that can stem from the extirpation or overabundance of large mammals (MacLean *et al.* 2011). Both increases (bush encroachment) and loss (land degradation) of woody vegetation cover resulting from excessive grazing by livestock are major concerns in savannas and rangelands managed for cattle production (van Vegten 1983; Scholes & Archer 1997; Roques, O'Connor & Watkinson 2001; Tobler, Cochard & Edwards 2003). In our study site, where the native browsers are allowed to coexist with domestic cattle, we found no evidence for changes in woody biomass and cover over a decade, and clear evidence that shrub encroachment would accelerate rapidly if native browsers were removed. These results show that native browsing ungulates provide a critical ecosystem service by suppressing shrub encroachment on rangelands managed for cattle production.

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